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LONG-TERM VEGETATION DYNAMICS OF THE LOWER STRATA OF A WESTERN MASSACHUSETTS OXBOW SWAMP FOREST

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ABSTRACT. The structure, composition, and floristics of understory swamp forest vegetation in Ned's Ditch, a segment of a regularly flooded oxbow in Northampton, Massachusetts, has been investigated at intervals from 1973 through 1996. The forest canopy is dominated by *Acer saccharinum* in association with *Quercus palustris* and *Fraxinus pennsylvanica*; these species are regenerating despite the deaths of a number of trees between 1975 and 1985. The shrub stratum, dominated by *Cephalanthus occidentalis*, has remained relatively unchanged. In the herbaceous stratum, species abundances fluctuate from year to year in relation to flooding and other aspects of hydrology with aquatics such as *Lemna minor* increasing during wet years and annuals, particularly *Bidens* spp., growing to maturity in times of drought. The abundance of *Osmunda regalis* and *Onoclea sensibilis* has remained relatively constant over the 23 year period, but tree seedlings have become increasingly important though few have been recruited to the upper strata. Overall, emergent and floating hydrophytes in the herb stratum have tended to decline although the composition of the flora of the herb stratum continues to strongly resemble the flora of adjacent marshes. These observations suggest that preserving and successfully managing Ned's Ditch and similar floodplain forests will require the maintenance of species of diverse ecological requirements adapted to a range of habitat conditions.

Key Words: swamp forest, floodplain vegetation, herbaceous flora, forested wetlands, Connecticut River, Massachusetts

Although the importance of forests along floodplains within river ecosystems has been increasingly recognized (Decamps

1996; Gregory et al. 1991), the dynamics of floodplain forest vegetation remain poorly understood. Not surprisingly, investigations of economically important floodplain forest trees (Jones et al. 1994; Megonigal et al. 1997; Robertson et al. 1978) have been more common than studies of floodplain herbs and shrubs (Menges and Waller 1983). Kearsley (1999a) has recently inventoried Massachusetts floodplain forests and devised a classification that includes understory species; however long-term studies of the composition and structure of lower floodplain forest strata continue to be scarce.

In western Massachusetts, studies of vegetation within Connecticut River oxbows have been in progress since 1969 (Robinton and Burk 1971). Four of these oxbows form an apparent chronosequence, a "spatial array" of sites of different ages (Barbour et al. 1987) in various stages of seral development ranging from open water through freshwater marsh to mature swamp forest (Holland and Burk 1990). The most thoroughly studied of these sites, Ned's Ditch, is the northwestern segment of an oxbow that was cut off from the main stream of the Connecticut River around 710 (±130) YBP as determined by stratigraphy and radiocarbon dating (Holland and Burk 1982). Now owned by the Massachusetts Audubon Society as a part of Arcadia Wildlife Sanctuary, Ned's Ditch contains one of the largest stands of floodplain swamp forest in New England. The vegetation of the area within the old river bed includes this forest, stands of buttonbush (*Cephalanthus occidentalis*), and relic marsh communities surrounding ponds and remnants of the abandoned channel of an adjacent stream (Holland and Burk 1984, 1990). Ned's Ditch is regularly flooded during periods of heavy precipitation and/or high water on the Connecticut River with floodwaters entering its eastern section from an adjacent oxbow that was cut off from the main stem of the Connecticut River in 1840 (Holland and Burk 1982). During unusually heavy flooding, floodwaters also enter from the channel of the Mill River on the western margin of Ned's Ditch. Studies conducted during the period 1973–1977 (Holland and Burk 1984) indicated that the canopy trees, particularly the most prominent species, *Acer saccharinum, Quercus palustris,* and *Fraxinus pennsylvanica,* were well represented by seedlings in the understory and apparently replacing themselves. Hence the Ned's Ditch forest community was thought to be in a state of "hydric disclimax" (Daubenmire 1968) or "pulse stability" (Odum 1969) that might persist indefinitely (Holland and Burk 1984).

A resampling of the Ned's Ditch canopy in 1985, however (Holland and Burk 1986), indicated that a number of trees of all species had died since 1975, with highest mortalities in the lower size classes (3.0–13.5 cm diameter). In addition, recruitment from the herb stratum had been extremely low. Comparable tree deaths and low recruitment were also observed by studies in a regularly flooded oxbow in Hatfield, Massachusetts, a "younger" stage in the oxbow chronosequence (Holland 1998; Holland and Burk, in press), but not in an "older" rarely flooded stage on a higher Connecticut River terrace in Whately, Massachusetts (Holland and Burk 1986, in press, and unpubl. data). Field studies a decade later in Ned's Ditch indicated that few canopy trees died between 1985 and 1995/96. Nonetheless, although seedlings of *Acer saccharinum, Quercus palustris,* and *Fraxinus pennsylvanica* were abundant, few trees had been recruited into the smaller stem classes of the canopy (Burk et al. 1996).

This study compared the shrub and herb strata of Ned's Ditch during the interval 1973–1977 with their state in 1985 and again in 1995/96. Specific goals of the study were:

(1) to document the abundance and distribution of the vascular plant species comprising the shrub and herb strata of the Ned's Ditch swamp forests throughout this 23 year interval;
(2) to assess changes in the abundance and distribution of vascular plant species in these strata throughout the study period;
(3) to attempt to identify long-term changes in vegetation between 1973 and 1995/96, and to distinguish long-term changes from changes that reflect short-term fluctuations in hydrological conditions, including drought and flooding;
(4) to examine relationships between the vegetation of the lower strata of the swamp forest and the vegetation of adjacent marshes.

MATERIALS AND METHODS

Quantitative sampling of the canopy, shrub, and herb strata of the Ned's Ditch forest was initiated in the summer of 1973 and repeated during 1974, 1975, 1977, 1985, and 1995–1996. Quantitative sampling of marsh vegetation in Ned's Ditch was conducted in 1973, 1974, 1975, 1984, and 1994.

As a part of the 1973 sampling, five transects were laid out at 285 m intervals across Ned's Ditch, beginning near its eastern margin. Each transect extended from the old Connecticut River bank through the former river bed to the opposite bank, a distance of approximately 306 m. Along each transect, swamp forest vegetation occurred within the former Connecticut River bed, adjacent to the old Connecticut River bank on both sides but at a lower elevation. Stands of buttonbush swamp and ponds with relict marsh communities occurred farther towards the centers of the transects; transitions between swamp forest and the buttonbush swamp and marsh communities were abrupt and boundaries between each vegetation type were easily delimited.

To sample swamp forest vegetation, ten 10 m × 10 m permanent plots were established, two on each transect beginning 3.3 m in from the edge of the forest closest to the bank at each end. In 1996, the four corners of each plot were marked with buried rebar which could be re-located by means of a metal detector during successive sampling periods. The shrub stratum in each plot was sampled within a 5 m × 5 m quadrat located in one corner of each plot. Presence and coverage were estimated for each woody vascular plant species occuring as a shrub or sapling. To sample the herbaceous stratum within each 10 m × 10 m plot, ten 1 m × 1 m quadrats were laid out, five at regular intervals along the transect and five at regular intervals along a baseline perpendicular to the transect. Presence and coverage as determined by visual estimate were noted for all vascular plants including herbs, vines, and woody seedlings under 60 cm height in each of the 100 smaller quadrats. In addition the presence and cover of the aquatic moss *Amblystegium riparium* (Hedw.) BSG. (Amblystegiaceae) was also recorded for each smaller quadrat. Sampling of the ten 5 m × 5 m shrub quadrats was conducted during July and August of 1973, 1975, and 1985. Because of time constraints, six shrub quadrats were sampled in July and August of 1995 and the remaining four in 1996. Sampling of all 100 1 m × 1 m quadrats was conducted during July and August of 1973, 1974, 1975, 1977, and 1985. Sampling of 60 smaller quadrats within six 10 m × 10 m plots was conducted in 1995 and the remaining 40 smaller quadrats within the four other 10 m × 10 m plots were sampled in 1996. During each sampling

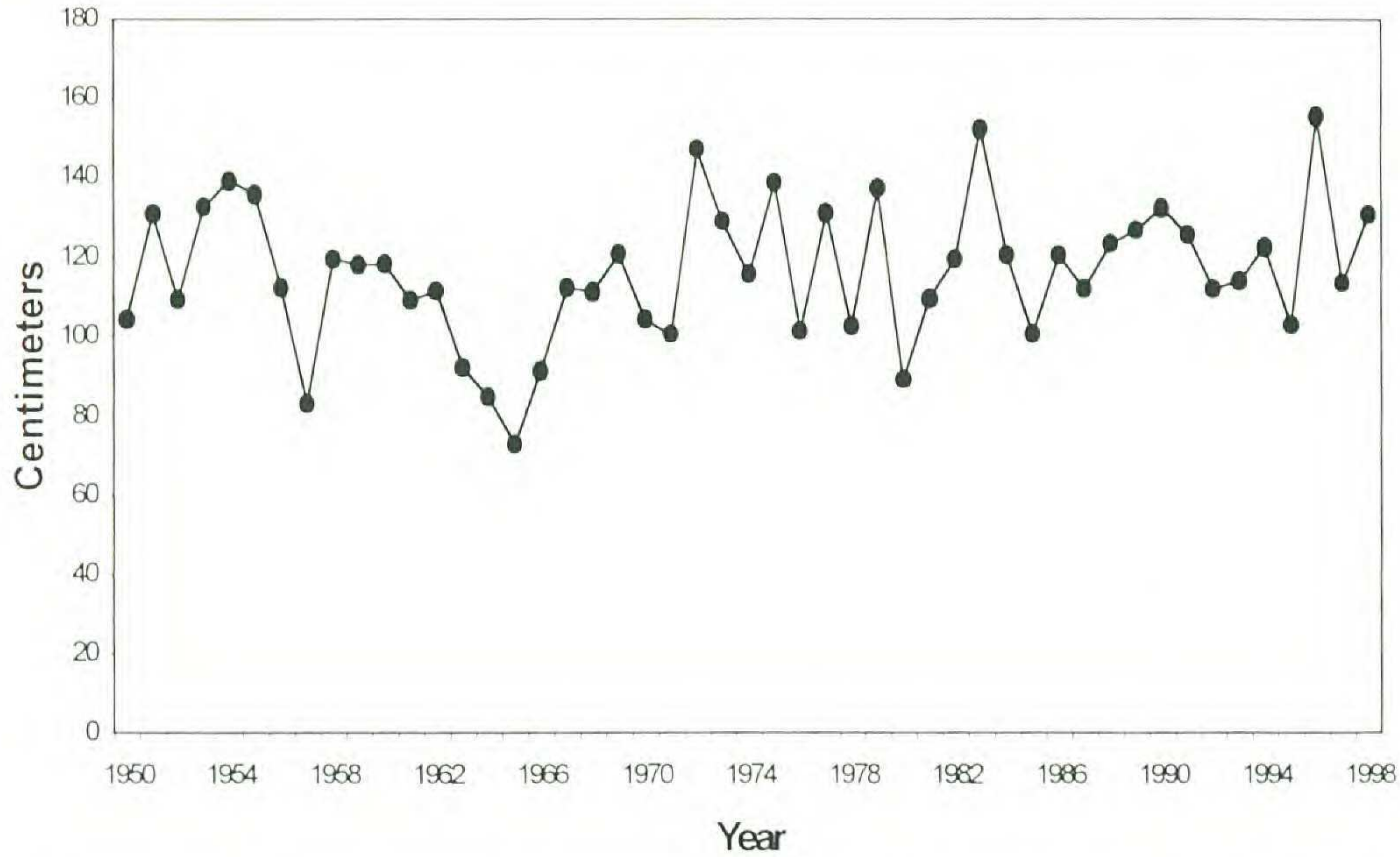

Figure 1. Total annual precipitation (cm) in the study area, 1950 through 1998. See text for sources.

period, studies of the shrub and herb strata were coordinated with sampling of the canopy within each plot.

In some instances, particularly in years when growth was delayed or disrupted by late spring or summer flooding, a number of very small plants in the quadrats could be identified only at the generic level. Because of this, immature specimens of several regularly or sporadically encountered genera that might be represented in the sampling by more than one species are grouped together under their respective genera. Nomenclature of fern species follows *Flora of North America North of Mexico* (Flora of North America Editorial Committee 1993). Nomenclature of seed plants follows Fernald (1950) except for *Bidens tripartita* L. to include *B. comosa* (A. Gray) Wieg. and *B. connata* Muhl. Voucher specimens have been deposited in SCH.

For analysis and comparison, average percent cover and frequency were recorded for each species with cover values rounded off to the nearest whole number. Summed cover values for each year's sampling were calculated using actual rather than rounded data. Species richness, the total number of species present in each stratum, was calculated by counting all species present. Species grouped to genera as a single unit were counted only once in determining richness. For example, seedlings listed as *Cornus* spp. were counted as such, even though mature specimens of *C.*

alternifolia L.f., *C. amomum* Miller, and *C. stolonifera* Michx. were present at the site as potential seed sources. Discussions of the value of cover and frequency data in assessing vegetational change are in Daubenmire (1968) and Mueller-Dombois and Ellenberg (1974), and are summarized with reference to the adjacent oxbow marshes in Holland and Burk (1990).

The permanent plots and all quadrats were systematically placed, and we have attempted to re-locate each individual quadrat at each sampling period; hence probability statistics cannot be used as aids in interpreting the data (Barbour et al. 1987; Mueller-Dombois and Ellenberg 1974). As in earlier studies of changes in floristic composition over a series of collecting periods (Holland and Burk 1990; Holland and Sorrie 1989; Lauermann and Burk 1976), the Simpson Index of Resemblance (Simpson 1965) was used to compare the taxonomic composition of the herb stratum in successive years of sampling. Simpson's Index of Resemblance (100 c/n1, in which c is the number of species common to the two floras and n1 is the number of species in the smaller flora) is helpful in comparing floras of approximately equal sizes in a common area. In addition, to assess interrelationships between the composition of the Ned's Ditch swamp forest and floras of adjacent Ned's Ditch marshes, Simpson's Index was also used to compare the swamp forest in 1977, 1985, and 1995/96 with the composition of the Ned's Ditch marshes. The marshes were sampled in 1974 and 1984 (Holland and Burk 1990) and again in 1994, one year prior to the sampling of the forest (Holland and Burk, unpubl. data).

Data on yearly precipitation (Figure 1) were obtained from the website www.ncdc.noaa.gov/onlineprod/drought/temp/drought_15006 for western Massachusetts from 1950 through 1998. Data on the times of major flooding were obtained from our own observations of the site.

RESULTS

As in earlier studies (Holland and Burk 1984, 1990) tables were prepared listing all vascular plant species in any quadrat for each sampling period. Data from 1973 are available in Sackett (1974) and data from 1973, 1974 and 1975 in Sackett (1977). The 1975 data are also included in Holland and Burk (1984) with an indication of species sampled earlier but not in 1975 and spe-

Table 1. Composition of the herb stratum in Ned's Ditch in 1977, 1985, and 1995/96. Numbers represent mean and standard deviation (in parentheses) of percent cover (C), frequency (F), and total number of species sampled. [1]mostly *B. tripartita* L. and *B. cernua* L., [2]mostly *S. nigra* Marshall.

Species	1977		1985		1995/96	
	C	F	C	F	C	F
Herbs and vines						
Agrostis alba L.	<0.5 (0.83)	4	—	—	—	—
Agrostis perennans (Walter) Tuckerman	1 (3.25)	11	—	—	—	—
Alisma subcordatum Raf.	<0.5 (0.88)	5	<0.5 (0.06)	1	<0.5 (0.66)	4
Apios americana Medikus	3 (8.14)	11	7 (14.68)	19	2 (4.34)	16
Arisaema triphyllum (L.) Schott	<0.5 (0.48)	5	<0.5 (0.13)	5	<0.5 (0.72)	8
Bidens frondosa L.	4 (4.85)	61	3 (6.27)	34	<0.5 (0.68)	14
Bidens spp.[1]	<0.5 (0.70)	18	7 (5.24)	75	<0.5 (0.16)	8
Boehmeria cylindrica (L.) Swartz	1 (1.35)	46	4 (7.97)	50	2 (4.46)	19
Cardamine pensylvanica Muhl.	<0.5 (0.28)	6	<0.5 (0.02)	1	—	—
Carex tribuloides Wahlenb.	3 (10.25)	10	<0.5 (0.20)	<0.5	—	—
Carex spp.	1 (1.12)	18	<0.5 (0.27)	<0.5	1 (1.24)	7
Celastrus scandens L.	—	—	<0.5 (0.03)	1	—	—
Cicuta bulbifera L.	—	—	<0.5 (0.17)	6	—	—
Cuscuta gronovii Willd.	—	—	<0.5 (0.03)	1	—	—
Dryopteris carthusiana (Villars) H. P. Fuchs	1 (2.14)	3	1 (2.37)	4	—	—
Dulichium arundinaceum (L.) Britton	<0.5 (0.09)	5	<0.5 (0.13)	4	—	—
Echinochloa crusgalli (L.) P. Beauv.	—	—	<0.5 (0.03)	1	—	—
Eleocharis acicularis (L.) Roemer & Schultes	6 (13.4)	25	<0.5 (0.16)	16	1 (1.26)	5
Erechtites hieracifolia (L.) Raf.	—	—	<0.5 (0.52)	9	—	—
Eupatorium spp.	<0.5 (0.32)	1	—	—	—	—

Table 1. Continued.

Species	1977		1985		1995/96	
	C	F	C	F	C	F
Galium spp.	1 (0.54)	31	1 (1.52)	32	<0.5 (0.47)	9
Geum virginianum L.	—	—	<0.5 (0.22)	6	—	—
Glyceria fernaldii (Hitchc.) St. John	—	—	12 (14.56)	54	3 (6.25)	20
Hieracium spp.	—	—	<0.5 (0.04)	2	—	—
Hypericum virginicum L.	<0.5 (0.09)	1	<0.5 (0.88)	7	<0.5 (0.19)	2
Impatiens capensis Meerb.	<0.5 (0.09)	3	<0.5 (0.68)	6	<0.5 (0.16)	4
Leersia oryzoides (L.) Swartz	1 (1.44)	11	<0.5 (0.90)	15	—	—
Lemna minor L.	4 (7.71)	36	<0.5 (0.14)	3	<0.5 (0.22)	26
Ludwigia palustris (L.) Ell.	1 (2.35)	25	<0.5 (0.14)	17	—	—
Ludwigia polycarpa Short & Peter	<0.5 (0.69)	2	<0.5 (0.40)	2	—	—
Lycopus uniflorus Michx.	—	—	—	—	<0.5 (0.68)	10
Lycopus virginicus L.	<0.5 (0.19)	5	<0.5 (1.10)	5	<0.5 (0.47)	1
Lysimachia ciliata L.	<0.5 (0.13)	5	<0.5 (0.13)	1	—	—
Lysimachia nummularia L.	<0.5 (0.06)	2	<0.5 (0.13)	3	1 (0.89)	9
Lysimachia terrestris (L.) BSP.	1 (0.84)	13	1 (1.09)	25	1 (1.09)	11
Onoclea sensibilis L.	6 (13.97)	13	5 (9.27)	27	6 (14.72)	18
Osmunda regalis L.	5 (10.47)	15	8 (16.27)	13	6 (10.94)	14
Panicum clandestinum L.	<0.5 (0.54)	3	—	—	—	—
Parthenocissus quinquefolia (L.) Planchon	—	—	—	—	<0.5 (0.22)	6
Penthorum sedoides L.	1 (2.74)	8	<0.5 (0.14)	3	—	—
Phalaris arundinacea L.	—	—	<0.5 (0.28)	2	—	—
Pilea pumila (L.) A. Gray	<0.5 (0.68)	16	—	—	—	—
Polygonum amphibium L.	—	—	1 (1.64)	6	—	—
Polygonum hydropiperoides Michx.	—	—	<0.5 (1.22)	7	—	—

Table 1. Continued.

Species	1977 C	1977 F	1985 C	1985 F	1995/96 C	1995/96 F
Polygonum punctatum Elliott	<0.5 (0.82)	9	—	—	—	—
Polygonum spp.	<0.5 (0.03)	1	—	—	<0.5 (0.16)	2
Prunella vulgaris L.	—	—	<0.5 (0.02)	1	—	—
Ranunculus flabellaris Raf.	8 (10.54)	38	1 (0.67)	40	<0.5 (0.82)	12
Rhus radicans L.	<0.5 (0.04)	2	<0.5 (0.18)	9	1 (2.78)	6
Sagittaria latifolia Willd.	—	—	<0.5 (0.19)	1	—	—
Scutellaria lateriflora L.	1 (0.75)	23	1 (1.02)	18	<0.5 (0.44)	6
Sium suave Walter	1 (0.97)	17	1 (1.25)	43	<0.5 (1.00)	7
Smilax herbacea L.	<0.5 (0.28)	3	<0.5 (0.35)	3	<0.5 (0.32)	1
Solanum dulcamara L.	—	—	<0.5 (0.25)	6	<0.5 (0.16)	2
Solidago spp.	<0.5 (0.03)	1	—	—	—	—
Spirodela polyrhiza (L.) Schleiden	<0.5 (0.32)	8	—	—	—	—
Thelypteris palustris Schott	—	—	—	—	2 (4.60)	5
Woody seedlings						
Acer saccharinum L.	9 (6.03)	77	8 (8.90)	78	7 (9.64)	60
Alnus rugosa (DuRoi) Sprengel	—	—	<0.5 (0.06)	1	—	—
Catalpa speciosa Warder	—	—	<0.5 (0.02)	1	—	—
Cephalanthus occidentalis L.	7 (5.36)	62	5 (4.92)	60	3 (2.62)	37
Cornus spp.	1 (0.99)	20	<0.5 (0.73)	4	<0.5 (0.81)	4
Fraxinus pennsylvanica Marshall	2 (3.06)	51	2 (3.00)	36	3 (3.94)	42
Ilex verticillata (L.) A. Gray	1 (1.24)	13	<0.5 (0.33)	5	<0.5 (0.47)	1
Populus deltoides Marshall	—	—	<0.5 (0.05)	2	—	—
Quercus palustris Muenchh.	1 (2.36)	7	<0.5 (0.28)	19	1 (1.28)	17
Robinia pseudoacacia L.	<0.5 (0.38)	14	—	—	<0.5 (0.06)	11
Salix spp.[2]	<0.5 (0.35)	7	<0.5 (0.03)	1	<0.5 (0.02)	1

Table 1. Continued.

	1977		1985		1995/96	
Species	C	F	C	F	C	F
Ulmus rubra Muhl.	<0.5 (0.05)	3	<0.5 (0.09)	10	<0.5 (0.25)	8
Viburnum recognitum Fern.	—	—	—	—	<0.5 (0.06)	1
Vitis spp.	1 (1.39)	27	2 (2.67)	24	1 (2.20)	5
Total species	50		57		39	

cies not in any quadrat but present elsewhere in swamp forest at the site. Data from 1977, 1985, and 1995/96, all previously unpublished, are included here in Table 1.

Despite the changes in the canopy of the Ned's Ditch swamp forest that were evident by 1985 (Burk et al. 1996; Holland and Burk 1986), the shrub stratum has remained relatively unchanged during the interval 1973–1995/96 (Table 2). Coverage of the dominant *Cephalanthus occidentalis* declined between 1973 and 1975 but returned to near 1973 levels by 1985. A decline of *Acer saccharinum* and *Fraxinus pennsylvanica* observed in the 1995/96 sampling of the shrub stratum probably reflects the recruitment of saplings of these tree species from the shrub stratum into the canopy.

Changes in the herb stratum for the period 1973 through 1977 were presented in Holland and Burk (1984). Within the herb stratum, total vegetative cover rose from a low of 14% in 1973 to 71% by 1975 and continued at a slightly higher level through 1977. The very low cover in 1973 resulted from damage caused by an atypical flood that had completely inundated the herb stratum for at least ten days in early July, less than a month before the sampling period (Holland and Burk 1984). Species richness rose from a low of 27 in 1973 to 47 by 1975 (Holland and Burk 1984) and continued at a somewhat higher level through 1977 (Table 1).

Total cover in the herb stratum remained relatively constant from 1975 through 1985 and then declined over the next ten year period (Table 3). Overall cover was lowest in years with late spring or summer floods and highest in wet years without late spring or early summer flooding. Species richness reached a high of 57 species in 1985 but had declined to 39, little above its 1974 level by 1995/96 (Table 1). The higher diversity in 1985 resulted, in part, from the presence of weedy species such as *Erechtites hieracifolia* and *Prunella vulgaris,* which had become established in small numbers under the unusually dry conditions of that season, and possibly, in part, because of the higher light levels in lower strata resulting from the extensive mortalities among canopy trees. Most invaders of this sort did not persist through 1995/96 (Table 1).

From 1977 through 1995/96, the abundance of the prominent rhizomatous ferns, *Onoclea sensibilis* and *Osmunda regalis* remained relatively constant, presumably in large part because the

Table 2. Variation in the cover of shrubs in Ned's Ditch. Numbers represent mean and standard deviation (in parentheses) of percent cover of each vascular plant species and percent total cover.

Species	Year			
	1973	1975	1985	1995/96
Acer saccharinum	8 (15.22)	11 (31.35)	8 (15.10)	1 (1.75)
Alnus rugosa	—	<0.5 (0.32)	<0.5 (0.63)	<0.5 (0.95)
Cephalanthus occidentalis	37 (32.65)	20 (26.38)	33 (31.24)	35 (39.08)
Cornus spp.	5 (5.77)	4 (4.86)	<0.5 (0.95)	2 (4.83)
Fraxinus pennsylvanica	—	2 (4.69)	8 (23.68)	<0.5 (0.34)
Ilex verticillata	1 (2.71)	2 (5.25)	4 (6.34)	5 (11.07)
Quercus palustris	1 (1.63)	<0.5 (0.42)	—	—
Salix spp.	—	1 (3.48)	—	—
Viburnum recognitum	—	<0.5 (0.32)	—	—
Vitis spp.	<0.5 (1.26)	1 (1.90)	—	4 (11.01)
Total cover (%)	52	45	54	48

Table 3. Variation in percent relative cover of vascular plant species in the herb stratum of Ned's Ditch. Relative cover of species at 5% or more total cover at any sampling period and total cover—see discussion of *Amblystegium riparium* in text.

Species	Year and Hydrology					
	1973 July Flood	1974 Dry	1975 Wet	1977 Wet	1985 Dry	1995/96 Dry/Wet
Acer saccharinum	7	11	6	12	11	17
Apios americana	1	<0.5	1	3	10	5
Bidens spp.	<0.5	1	1	4	14	2
Boehmeria cylindrica	<0.5	<0.5	<0.5	1	5	4
Cephalanthus occidentalis	1	8	6	10	7	6
Dulichium arundinaceum	29	17	10	<0.5	<0.5	0
Eleocharis acicularis	1	3	3	8	<0.5	1
Fraxinus pennsylvanica	1	1	1	2	3	6
Glyceria fernaldii	—	—	—	—	16	7
Lemna minor	7	3	48	7	<0.5	<0.5
Onoclea sensibilis	14	11	1	8	7	15
Osmunda regalis	14	14	4	7	11	14
Ranunculus flabellaris	1	3	3	11	1	1
Total cover (%)	14	36	71	73	74	43

same clones have been encountered at each sampling period. In addition, three major trends were noted within the vegetation of the herb stratum:

(1) The relative abundances of the more important species continued to fluctuate from year to year, apparently in relation to hydrology (Figure 1; Table 3). Hydrophytes increased during wet years such as 1975 and 1977 (Holland and Burk 1984). During dry seasons, annuals, particularly *Bidens* spp. grew to maturity and, while flowering, achieved "aspect dominance" (Oosting 1956) as in 1985 (Table 3 and field observations during dry years when sampling was not conducted).
(2) The relative cover of tree seedlings, particularly seedlings of *Acer saccharinum* and *Fraxinus pennsylvanica* increased (Table 3). In 1973, *Dulichium arundinaceum, Onoclea sensibilis,* and *Osmunda regalis* were the most prominent species, in descending order of abundance. By 1995/1996, *A. saccharinum* was most abundant, followed by *Onoclea sensibilis* and *Osmunda regalis.*
(3) Hydrophytes generally declined from previous levels of abundance. These included both "errant hydrophytes" (Mueller-Dombois and Ellenberg 1974) such as *Lemna minor, Ranunculus flabellaris,* and *Spirodela polyrhiza* (Table 1), and emergents. *Potamogeton pectinatus* L. and *Utricularia vulgaris* L. were sampled in 1975 (Holland and Burk 1984) but not later. A nonvascular errant hydrophyte, the moss *Amblystegium riparium* was present at every sampling period in the 1970s, reaching a peak cover of 21% of the total substratum in 1977, occurring in 81% of the quadrats sampled. The peak abundance of *A. riparium* appeared to be inversely related to the abundance of *L. minor,* which had reached its maximum in 1975 and declined by 1977 (Table 3). *Amblystegium riparium* was not seen during 1985, a dry season, nor identified in 1995; it was encountered again in nearly half the plots sampled in 1996 with an average cover of 2% of the substratum.

Several emergent hydrophytes also found in the high- and mid-marsh zones of the adjacent ponds declined markedly as well. *Dulichium arundinaceum,* the most abundant species of the herb stratum in 1973 and 1974, was present only at very low levels

Table 4. Simpson's Index of Resemblance comparing the flora of the Ned's Ditch swamp forest herb stratum at each sampling period to the flora of successive samplings of that stratum.

Year of Initial Sampling	Years of Successive Sampling				
	1974	1975	1977	1985	1995/96
1973	88.9	81.5	77.8	70.4	63.0
1974		77.8	83.3	77.8	63.9
1975			72.3	70.2	74.4
1977				72.9	81.6
1985					81.6

in 1977 and 1985 and not sampled at all in 1995/96. *Eleocharis acicularis* persisted at generally low levels throughout the period, reaching its greatest abundance in 1977 and then declining.

Table 4 compares the herb flora of Ned's Ditch at each sampling period from 1973 to 1985 to the floras of successive sampling periods at the specific level. Floras from sampling periods closer in time tended to be more similar than floras from longer intervals, and the least similar floras were those of the first and last collections of data, 1973 and 1995/96. When Ned's Ditch marshes were compared with the swamp forest herb stratum in successive years of sampling, similarities tended to be higher when comparisons were made between marsh and forest floras at the closer time intervals (Table 5). Levels of forest/marsh similarity fall within the range of forest/forest similarities. The Simpson Index comparing the composition of the Ned's Ditch swamp forest in 1974 with the forest in 1995/96 is identical with Simpson's Index comparing the Ned's Ditch marsh in 1974 with the forest in 1995/96.

Table 5. Simpson's Index of Resemblance comparing the flora of the Ned's Ditch marshes to the herbaceous flora of the adjacent swamp forest herb stratum at each successive sampling.

Year of Marsh Sampling	Years of Swamp Forest Sampling			
	1973/75	1977	1985	1995/96
1974	75.8	75.0	72.2	63.9
1984			74.1	71.1
1994				79.5

DISCUSSION

Fluctuations in the composition of the herb stratum of Ned's Ditch in response to seasonal variations in hydrology may represent a community response to conditions associated with a particular form of hydric disclimax, i.e. a persistent state maintained by recurrent but irregular flooding. During wet seasons, hydrophytic species become abundant; during dry seasons these are largely replaced by mesophytic forms (Holland and Burk 1984). Together the understory flora represents a spectrum of life forms including annuals, woody seedlings, emergent perennial graminoids, perennial forbs, errant hydrophytes, annuals, and vines.

Previous comparisons of the herb stratum of the Ned's Ditch swamp forest to the floras of adjacent marshes have shown a stronger resemblance than that of other oxbow swamp forests and their marshes (Holland and Burk 1990). While the low marsh dominants *Nuphar variegata* Durand and *Potamogeton pectinatus* did not extend into the forest, many species were shared by both communities (Table 5), and despite the decline of hydrophytes in the swamp forest over the last two decades of the study, the floras of the marshes and the herb stratum of the forest continued to be strongly similar. In part this similarity reflects dispersal during periods of flooding when high water extended throughout the oxbow, connecting ponds and forest. In addition, the ponds occasionally dried out and species more frequently found in the forest became established on exposed pond bottoms.

The increased relative abundance of woody seedlings and overall decline in hydrophytes in Ned's Ditch may have resulted, in part, from drier conditions associated with changes in elevation resulting from sedimentation and from reduced available light on the forest floor associated with the growth of the canopy trees. Studies of comparable Wisconsin floodplain forests have characterized *Bidens* spp. and *Lemna* spp. as high-light specialists at the lowest elevations of the herb strata and *Acer saccharinum* and *Onoclea sensibilis* as light generalists at somewhat higher elevations; seedlings of *A. saccharinum* have been shown to germinate well in either light or shade (Peterson and Bazzaz 1984). Scouring through heavy flooding and high mortalities of the dominant trees before 1985 (Burk et al. 1996) may have slowed or reversed these trends since long periods of flooding are particularly harmful to young seedlings of *A. saccharinum* (Peterson and Bazzaz 1984).

Similar effects of different flood regimes have also been observed in Louisiana swamp forests that contain understory species in common with Ned's Ditch (Conner and Day 1976). Stands that were flooded to a depth of 0.6 m much of the year possessed constantly saturated soil and herb strata containing only floating and emergent aquatics, including *Lemna minor* and *Spirodela polyrhiza.* Forests that were inundated for two to three months in the spring but surface-dry in summer supported more diverse lower strata of "briars, grasses and annual herbs" along with seedlings, saplings, and woody vines.

Related studies (Conner et al. 1981) contrasted the effects of altered flood regimes in swamp forests that had shared similar vegetation and seasonal flooding through the 1950s. In an undisturbed control site, growth of aquatics and understory woody vegetation was limited by shading and periodic flooding. In a site now permanently flooded, the resultant deaths of canopy trees, particularly *Fraxinus* spp., increased light penetration and allowed the spread of aquatics, including *Lemna minor* and *Spirodela polyrhiza.* After permanant inundation, flood-tolerant shrubs also invaded, including *Cephalanthus occidentalis,* the seeds of which are capable of germinating underwater (see references in Conner et al. 1981). In a site now managed by controlled winter/spring flooding followed by an annual summer/fall drawdown, aquatic species were absent. The managed site was increasingly dominated by *Acer rubrum* var. *drummondii* and *Fraxinus,* taxa with seeds that germinate during the dry period to produce seedlings that become established before flooding.

Since the initial sampling of vegetation in Ned's Ditch, the concept of a vegetation type that may persist indefinitely through "pulse stability" (Odum 1969) has been explored with reference to floodplain forests in particular. Odum et al. (1979), using data from Conner and Day (1976) for examples, have suggested that moderate or seasonal flooding may result in increased tree growth in mature floodplain forests composed of species already well adapted to the flooding regime. Continuous high levels of flooding, however, may result in impounded and stagnant conditions that stress canopy vegetation and reduce productivity. More recent studies (Megonigal et al. 1997) conclude that the results of flooding are complex and affected by the timing and length of floods and the relative strength of their flow. In addition, stresses resulting from drought and anaerobic soils may offset any benefits of flooding (Mitsch and Rust 1984).

CONSERVATION

The integrity of the Ned's Ditch swamp forest community is largely dependent on dynamic hydrological conditions resulting from periodic flooding on the Connecticut River. In 1973, at the time of the initial sampling, much of the site was privately owned and subject to intermittent logging, dumping of wastes, and other disruptive human activities. The entire Northampton oxbow including the Ned's Ditch forest is now owned by the Massachusetts Audubon Society and preserved as a natural area with a management plan (McGuire 1988) that includes control of potentially invasive exotic species. With the exception of *Lysimachia nummularia,* non-native species have not been regularly encountered in Ned's Ditch; although *Solanum dulcamara, Prunella vulgaris,* and seedlings of *Catalpa speciosa* were sampled in 1985, only *S. dulcamara* persisted until 1995. Nonetheless, a number of potentially invasive species, several of which are now frequently encountered in other Massachusetts floodplain forests (Kearsley 1999b) are well established nearby. These include *Acer platanoides* L., *Berberis thunbergii* DC, *Celastrus orbiculatus* Thunb., *Polygonum cuspidatum* Sieb. & Zucc., *Rhamnus frangula* L., and *Catalpa speciosa,* which is spreading along the Mill River at the western margin of Ned's Ditch (Burk and Prabhu 1988). Spread of these species should be monitored and, if necessary, curtailed because of their potential harm to native species (Weatherbee et al. 1998). Of particular concern is *Ludwigia polycarpa,* currently threatened in Massachusetts (Massachusetts Natural Heritage and Endangered Species Program 1997) and not seen at its former locations in Ned's Ditch since 1985 (Holland and Burk 1990).

Sustaining biological diversity may be particularly critical in ecosystems such as floodplain forests that experience seasonal or longer fluctuations in hydrology (Grime 1997; Keddy and Reznicek 1982). Our studies, along with other investigations of floodplain forest vegetation, suggest that preserving and successfully managing these communities will require the maintenance of species of diverse ecological requirements adapted to a range of habitat conditions. In these dynamic systems, individual species tend to fluctuate in abundance and may sometimes disappear completely from a given floodplain forest site. Hence a range of similar protected sites within the region may be essential in providing reservoirs from which species may be recruited as habitat conditions change. Since our earliest vegetation studies in Ned's Ditch, we have argued for the conservation of floodplain forests and other wetland habitats (Holland and Burk 1984, 1990); and Kearsley's recent inventory (Kearsley 1999a) reinforces the necessity for maintaining these increasingly scarce plant communities, particularly transitional and "Small-river" floodplain forests, few of which are now protected, on a broader scale within the state and region.

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